

The male postabdomen of the “ancestral” archostematan beetle *Tetraphalerus bruchi* Heller, 1913 (Ommatidae) and its phylogenetic significance

Frank Hünefeld^{a,*}, Adriana E. Marvaldi^b, Bianca Müller^a, John F. Lawrence^c, Rolf Georg Beutel^a

^aInstitut für Spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller-Universität Jena, Erbertstr. 1, D-07743, Jena, Germany

^bInstituto Argentino de Investigaciones de Zonas Áridas (IAZI), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), C.C. 507, 5500 Mendoza, Argentina

^cJohn Lawrence, 12 Hartwig Road, Gympie QLD 4570, Australia

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ABSTRACT

External and internal features of the male postabdomen of *Tetraphalerus bruchi* were examined with a broad spectrum of morphological techniques and are described in detail. The conditions found in males of *Tetraphalerus* are compared to those in other archostematan beetles and members of other coleopteran suborders. The far-reaching reduction of the sternite I, structural modifications of sternite II, the retracted condition of the terminal segments, and ventromedially fused apodemes arising from the anterior margin of tergite IX are likely autapomorphies of Coleoptera. The male postabdomen of *Tetraphalerus* is less derived than in most other groups of Coleoptera. The sclerotized elements are symmetrical. In contrast to earlier statements on the archostematan male genital apparatus a distinctly developed, sclerotized basal piece is present. The aedeagus is trilobed and all elements of the copulatory apparatus are distinct. The muscular equipment is simple and moderately developed. All muscles (except the transverse muscles 61 and 62) occur pairwise and symmetrically. The distinct increase of the number of postabdominal muscles in representatives of the higher lineages of Coleoptera is likely linked with a torsion of the copulatory apparatus, which also results in asymmetries of the sclerotised parts. The testes of *Tetraphalerus* are long, multi-coiled tubes like in other archostematans, *Myxophaga* (*Torridincola*) and *Adephaga*. The presence of a deep notch on the parameres is a synapomorphy of *Tetraphalerus* and *Omma*. Curved parameres, a shortened distal portion, and a distinctly shortented penis are potential synapomorphies of *Omma rutherfordi* and *Omma mastersi*. The large size of the sclerotized part of the phallobase ('basal piece') and the division of the sclerotization of sternum IX are potential groundplan autapomorphies of Archostemata, with secondary modification of the latter feature in Cupedidae. The reduced condition of the sclerotization of sternum VIII is an apomorphic condition which has likely evolved independently in *Tetraphalerus* and *Paracupes*. Further anatomical investigation of the male genital apparatus of Coleoptera and holometabolous insects in general is required for a reliable morphological and phylogenetic interpretation. Concerning the presence or absence of particular sclerotizations (e.g., 'basal piece' of phallobase) histological section series and Confocal Laser Scanning Microscopy can add more precise information to what can be observed using permanent preparations of macerated specimens.

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1. Introduction

It was pointed out in the classical work on the male genital tube by Sharp and Muir (1912) that copulatory structures were considered “bad guides in classification, although they are generally admitted to be of first importance for the discrimination of species”. The authors added that if “the extreme importance of the genital conduit be seized, it will appear that its structure must certainly be

of very great assistance in taxonomy”. Since the publication of this landmark study, male genitalia played a crucial role in numerous taxonomic studies, as implicitly predicted by Sharp and Muir (1912), but still play a very minor role in high level phylogenetic reconstruction. Characters of the male genitalia were completely omitted in recent high level phylogenetic analyses of coleopteran relationships (e.g., Beutel and Haas, 2000; Beutel et al., 2008; Friedrich et al., 2009). Only very few detailed anatomical treatments are available (e.g., Hieke, 1966; see below) and one of the very few comparative studies covering the entire Coleoptera (Iablokoff-Khnzorian, 1980) lacks any modern phylogenetic approach and does not provide comprehensible phylogenetic interpretations.

* Corresponding author.

E-mail address: frank.huenefeld@uni-jena.de (F. Hünefeld).

Tetraphalerus bruchi (Fig. 1), the species we chose for our investigation, belongs to the small archostematan family Ommatidae, arguably the most ancestral group of Coleoptera (e.g., Lawrence, 1999; Beutel et al., 2008). Like the other species of the genus, it occurs in very arid areas of northern Argentina. The larvae are still unknown and females are extremely rare. Adult males are collected on light traps in calm nights with temperatures above 25 °C in December or January.

Recent phylogenetic investigations (Beutel et al., 2008; Friedrich et al., 2009) have shown that *Tetraphalerus* and *Omma* (Ommatidae) likely form the sistergroup of all other extant archostematan groups, and Archostemata (including Jurodidae) the sistergroup of the remaining extant coleopteran suborders. The knowledge of the morphology of larvae and adults of Archostemata has dramatically increased during the last years (Beutel and Hörnschemeyer, 2002a,b; Beutel et al., 2008; Grebennikov, 2004; Hörnschemeyer, 2005; Hörnschemeyer, et al., 2002, 2006; Friedrich et al., 2009). However,



Fig. 1. *Tetraphalerus bruchi*, male scale bar = 5 mm.

the abdomen and the genital organs are still clearly understudied. The male terminal segments of *Priacma serrata* LeConte, 1861 were described by Edwards (1953a,b) and a brief account of the male genitalia of *Prolixocupes latreillei* Solier, 1849 and both species of *Tetraphalerus* was given by Vidal Sarmiento (1969), based on dissections of specimens relaxed in chloral lactophenol. The male genitalia are depicted and briefly described in the description of *Crowsoniella relicta* Pace, 1975 (Pace, 1975) and those of *Micromalthus debilis* LeConte, 1878 in the unpublished Habilitation thesis of Hörnschemeyer (2004). Brief descriptions of the genitalia of all known archostematan species are also given in the latter study, and characters of the postabdominal segments are also treated in a species level phylogeny of Archostemata (Hörnschemeyer, 2009). The musculature of the male genital segments and other internal softparts were not described in detail for any archostematan species, and for very few non-archostematan beetles (e.g., Hieke, 1966; Krell, 1996).

Considering the obvious key role of Archostemata in the phylogeny of Coleoptera (e.g., Beutel et al., 2008) and the tremendous importance of the male genitalia in beetle taxonomy and systematics (e.g., Sharp and Muir, 1912), it is surprising that the morphology of this system has been considerably neglected, especially concerning archostematan beetles and the musculature and other internal soft parts. This induced us to carry out this investigation of abdominal structures of *Tetraphalerus*. The main aim is to present a detailed description of external and internal features of the male postabdomen, including musculature and internal parts of the genital apparatus. As the presently available information on the anterior abdomen is also very insufficient we also include a brief description of the pregenital segments. The conditions found in *Tetraphalerus* are compared to those in other groups of archostemata and in members of the other coleopteran suborders. It is a major drawback that sufficiently detailed information is only available for a very limited sample of coleopteran and non-coleopteran taxa. Moreover, the homology of the sclerites involved in the formation of the aedeagus with terminal sclerites found in other endopterygote groups which lack an aedeagus in the proper sense (e.g., Neuropterida) is highly ambiguous. For these reasons we did not carry out a formal cladistic evaluation of our data at this point.

2. Materials and methods

2.1. Specimens examined

Two male specimens of *T. bruchi* (fixed in 100% ethanol) were studied in detail. Collection data: ARGENTINA, Mendoza province, Lavalle, Reserva Forestal Telteca, 16/17-XII-2005, light trap, coll. A. E. Marvaldi. Voucher specimens, from the same locality, are deposited in the entomological collection of IADIZA. For comparison males of the gyrid *Andogyrus columbicus* (fixed in Kahle's fluid) were examined.

2.2. Morphological techniques

External features were examined and drawn using a stereo microscope MZ 12.5 with a camera lucida (LEICA).

For semi-thin cross-section series one specimen of *T. bruchi* was embedded in Araldite CY 212® (Agar Scientific, Stansted/Essex, England) and cut at 1.0 µm with a diamond knife (Elementsix, Cuijk, Netherlands), using a microtome HM 360 (Microm, Walldorf, Germany). The sections were stained with Toluidin blue and Pyronin G (Waldeck GmbH and Co. KG / Division Chroma, Münster, Germany).

Pictures of all sections of the posterior abdomen were made using a Zeiss Axioplan (Göttingen, Germany) and the AnalySIS® documentation system (Soft Imaging Systems, Münster, Germany).

Figures were processed in Adobe Photoshop® and Adobe Illustrator® (San Jose, California, USA).

A three-dimensional reconstruction was carried out with Imaris (Bitplane AG, Zürich, Suisse) and MAYA7® software (Alias Wavefront, Toronto/Ontario, Canada) based on the cross-section series (Fig. 2).

A second specimen was macerated in KOH 5% for 24 h at room temperature. After maceration the terminalia were hyperextended and inflated with EtOH 100% for immediate hardening of the membranous parts. For this purpose a glass capillary was used, mounted in a micromanipulator system. This setup was recently developed for inflating the eversible parts of the aedeagus ('vesica') of small moths (Hünefeld et al., in preparation). Photographs of the prepared specimen were taken at a stereo microscope Zeiss Stemi SV 11 (Göttingen, Germany), using the AnalySIS® documentation system (Soft Imaging Systems, Münster, Germany). After this, the specimen was scanned with a confocal laser scanning microscope Zeiss LSM 510 (Göttingen, Germany). In a third step the specimen was dried to the critical point (EmiTech K850 Critical Point Dryer; Ashford, Kent, UK), coated with gold (EmiTech K500 sputter coater), and images were taken with a scanning electron microscope Philips XL 30 ESEM.

2.3. Terminology

The terminology for the exoskeleton and the internal parts of the genital system largely follows Lawrence et al. (2010). The term aedeagus is used to describe the entire complex formed by the phallobase, the parameres and the penis. A sclerotized element covering a ventro-median area or even lateral parts of the phallobase in several beetle groups is referred to as the "basal piece", as this term is widespread and consistently used amongst coleopterists. Stiffening

rods accompanied with the endophallus are referred to as "virga" (ventro-median) and "titillator" (lateral) following Matsuda (1976).

In this first survey of the postabdominal musculature of a male archostematan beetle the muscles are numbered and their sites of origin and insertion are described, accompanied by notes on the assumed function. The muscles are homologised with those described for members of other beetle subgroups (e.g., Hieke, 1966; Carabidae, Geotrupidae, Curculionidae; Krell, 1996; Scarabaeidae; Gyrinidae, own observations).

3. Results

3.1. External morphology

The abdomen is distinctly flattened dorsoventrally and approximately parallel-sided with the exception of the last exposed ventrite (Fig. 3). The terminal segments are invaginated in repose. The dorsal side is completely covered by the elytra at rest. Five ventrites are distinctly visible in ventral view, representing sternites III–VII. Their exposed ventral main part is almost completely flat, strongly sclerotised, and covered with roughly pentagonal tubercles bearing minute scale-like structures (see Beutel et al., 2008). On the dorsal side the hind margin is formed by the posterior edge of the partly invaginated tergite VIII (Fig. 3).

3.1.1. Pre-genital abdomen

Eight tergites are present below the elytra in resting position. Tergites I–VI are smooth and shiny, semitransparent and weakly sclerotised. Their transparent posterior margins overlap with the following tergite. An oblique, very elongate narrow spiracle is present laterally on tergite I (Fig. 3). Anteriorly it reaches the level of about mid-length of the metaventrite. Laterally, tergites III–VII

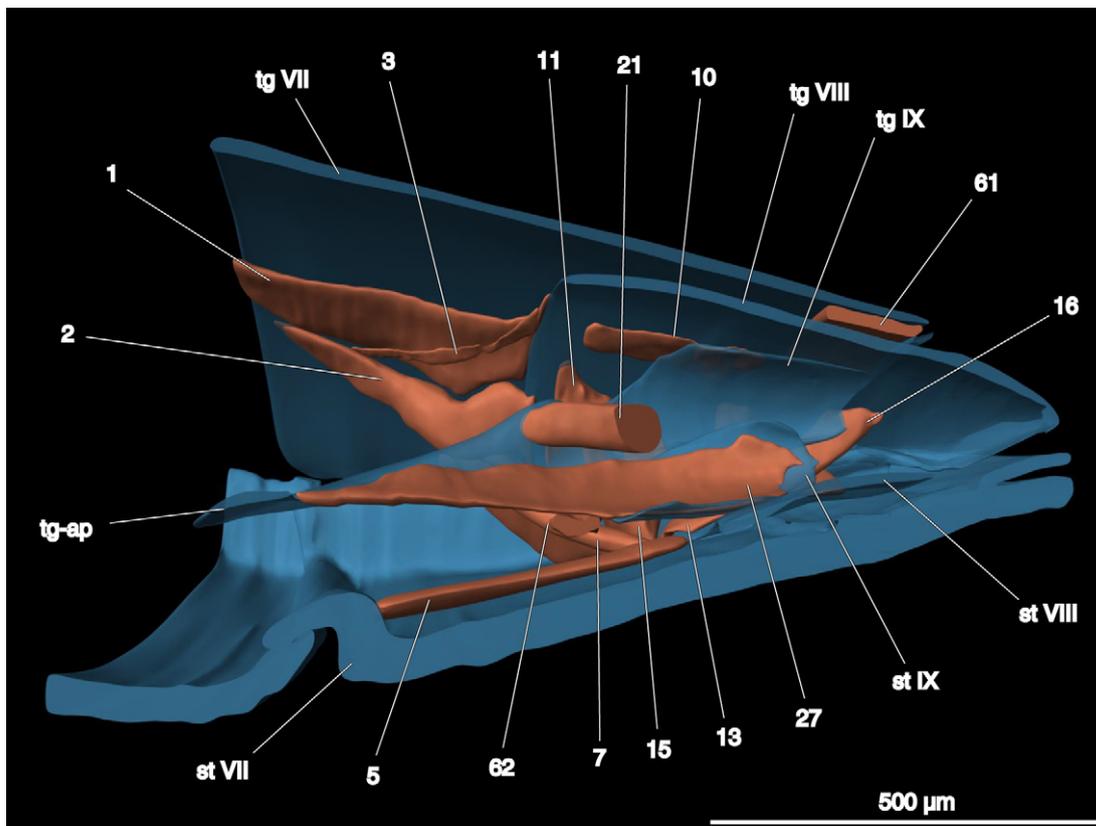


Fig. 2. *Tetraphalerus bruchi*, male abdomen, three-dimensional reconstruction, virtually cut along the medio-sagittal line. Gut, nervous system, aedeagus and internal softparts of the genital system are not shown. st, sternite; tg, tergite; and tg-ap, tergalapodeme.

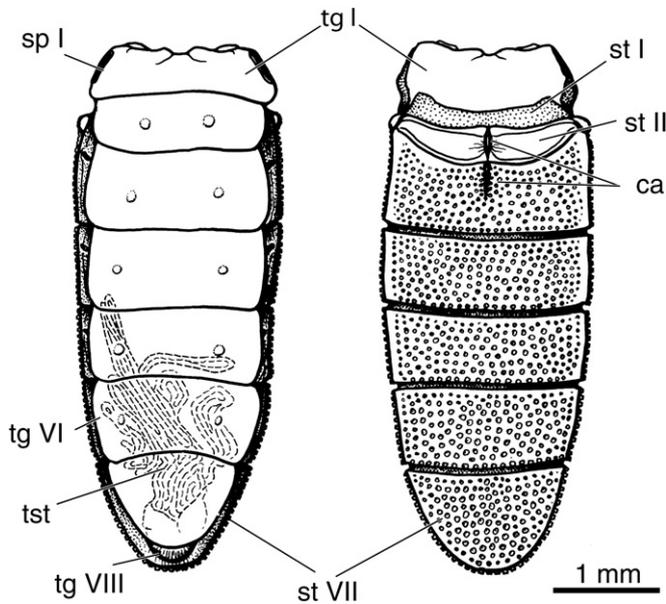


Fig. 3. *Tetraphalerus bruchi*, male abdomen, habitus. Dorsal (left) and ventral (right) view. ca, Carina; sp, spiracle; st, sternite; tg, tergite; and tst, testes.

are adjacent with whitish, semimembranous pleurites, which are about as broad as the laterosternites, and form a sharp angle with them. The border between the pleural and tergal elements is indistinct. Tergite VII is more strongly pigmented and sclerotised than the preceding ones. Its surface is covered with transparent setae. A very dense fringe of setae is present along the hind margin.

Sternite I is not recognisable as a separate sclerotised element (Fig. 3). Sternites II and III are firmly connected, but separated by a curved edge. Sternite II has a smooth surface and is completely covered by the metacoxae. Shallow concavities for reception of the coxae are medially separated by a high, strongly sclerotized carina (Fig. 3). Sternites III–VI (ventrites 1–4 in Fig. 3) are about 3 times as wide as long. The segmental borders are very slightly curved. A dense fringe of moderately long, transparent setae is present along the sharp lateral edge. Moderately broad, vertical laterosternites are present on segments III–VII. They are also densely covered with transparent hairs. Laterosternites III–VI are parallel-sided, whereas the sides of laterosternite VII are converging towards the abdominal apex. A distinct emargination is present at the anterior margin of sternite III, thus forming a concavity for reception of the metacoxae. Medially it bears a small carina, which fits in between the mesal metacoxal walls (Fig. 3). Laterally it forms a curved, horn-like projection, which fits into a posterolateral cavity of the metepimeron and is adjacent with the lateral metacoxal edge. It forms a concavity for reception of the femuro-tibial joint of the hind leg. Sternites III–VII are not overlapping. They are separated by deep recesses with a recognisable smooth stripe of cuticle on the deeper level, and internally connected by membranes (Fig. 3). Sternite VII is shield-shaped, apically rounded and seemingly ca. 1.2 times as long as the preceding ventrite (Fig. 3).

3.1.2. Genital and post-genital segments

Segment IX can be addressed as the genital segment in the strict sense as it bears the aedeagus with the genital opening. However, in this paragraph all segments are treated that show modifications related to copulation, starting with segment VIII. In repose, the terminal segments and their appendages are completely retracted into each other, and segment VIII is ventrally covered by sternite VII (Fig. 3). Tergite VIII is strongly sclerotised, distinctly smaller than the preceding segments, and evenly rounded posteriorly (Figs. 3 and 4).

It is partly invaginated and located distinctly below the hind margin of tergite VII (Fig. 3). Its surface is densely covered with transparent setae (Fig. 4). A pair of small ventrolateral sclerites is present in the posterior half of the region of sternum VIII (Fig. 4C–F). Their surface is smooth and glossy, and pores and setae or other specific structures of modifications are missing. The remaining parts of sternum VIII are membranous or extremely weakly sclerotized. The sclerotized part of tergite IX is entirely cleft along the dorso-median line (Figs. 4A–D and 7B). Its surface is smooth and devoid of setae. Its anteroventral corners are strongly protruded into long sclerotised stripes ('tergalapodemes') (Fig. 5 A and B), which are fused in the ventral midline, near the anterior border of the segment. Instead of a solid, plate-like sternite IX, a pair of large, trapezoidal sclerites are present, covering the posterior ventro-lateral areas of the segment (Fig. 4C–F). These sclerites are approximately twice as large as the corresponding sclerites on segment VIII, which are very similar in their surface structure. They are clearly separated from tergite IX by a portion of membranous cuticle. The phallobase is extensively sclerotized (basal piece), in particular ventro-laterally (Figs. 4 and 7E). This basal piece – sclerotization displays a conspicuous furrow along the ventro-median line (Figs. 4E and F, and 7E). The penis has the shape of a slender tube and appears slightly sinuate in lateral view, with the posterior portion pointing dorsad (Figs. 4 and 5A). A conspicuous dorso-median furrow is found on its posterior fourth (Figs. 4A–D, 5A and 6B). Approximately 15 large, rounded pores and slightly fewer small pores are present on both sides of it. The phallorema opens along the ventro-median line, near the apex of the penis (Fig. 7A). The simple endophallus is membranous and does not bear any sclerotized teeth ('cornuti'). In the resting position, the invaginated endophallus reaches approximately half-length of the penis anteriorly, where the ejaculatory duct opens at the primary gonopore. Inside the tube formed by the penis, a ventro-median, slender, sclerotized rod ('virga') is present, as well as a lateral pair of thin, elongated sclerites laterad the ejaculatory duct and the endophallus ('titillators'). The anterolateral margin of the penis is produced into a pair of stout apodemes (phallapodemes) that serve as attachment sites for muscles, which are responsible for the extrusion of the aedeagus (Figs. 5A, 6, and 7D, E). Laterad the penis, the parameres arise from the phallobase (basal piece in figures). They are only slightly shorter than the penis, and are distinctly divided into a large proximal and a small distal portion (1/4 of the total length of the paramere), both separated by a conspicuous furrow ('notch') (Figs. 4, 5A, 6B, 7B, C). The proximal portions are devoid of hairs or other surface structures. Only the small distal elements of the parameres show a light vestiture of very fine, minute setae (Fig. 4).

Segment X is almost completely retracted in segment IX, except the posteriormost part bearing the rectal opening (Fig. 4A–D). It can be easily distinguished in cross section images. Sclerotizations of segment X are a pair of slender dorso-lateral sclerite stripes ('bacculi') (Fig. 7B).

3.2. Musculature

A total of 18 muscles (Figs. 5 and 6) were identified in the male terminal segments of *T. bruchi*, starting with the intersegmental muscles between segments VII and VIII. In the following paragraph, the muscles are listed and described. The muscle numbers correspond with those in the figures and in Table 1. In contrary to other authors (Hieke, 1966; Krell, 1996) the muscle layers enclosing certain parts of the genital duct system and the accessory glands ('muscularis') are not treated as separate muscles in this section.

1: *M. antecosta-antecostalis uronotum medialis VII* (Figs. 5A–C and 6A). O. (=origin): anterior region of tergite VII, paramedially; I. (=insertion): anterior margin of tergite VIII, paramedially; F. (=function): retractor of segment VIII.

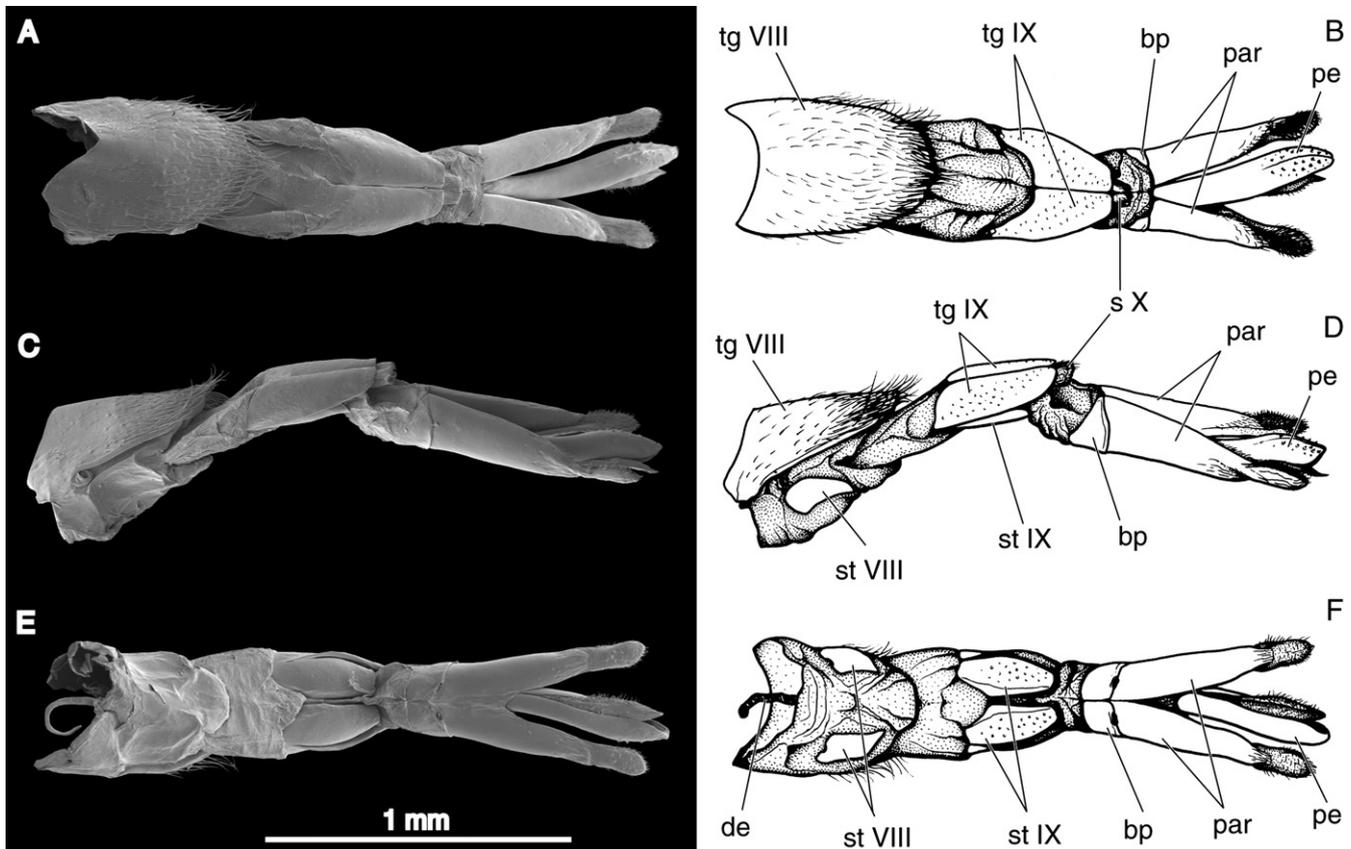


Fig. 4. *T. bruchi*, male postabdomen, hyperextended, SEM images (left) and corresponding line drawings (right). (A, B) Dorsal view; (C, D) lateral view; (E, F) ventral view. bp, Basal piece; de, ejaculatory duct; par, paramere; pe, penis; s, segment; st, sternite; and tg, tergite.

2: *M. antecosta-antecostalis uronotum lateralis VII* (Figs. 5A–C and 6A). O.: anterior region of tergite VII, close to the lateral margin; I.: anterior margin of tergite VIII, close to the lateral margin; F.: retractor of segment VIII.

3: *M. uronoto-antecostalis* (Figs. 5A–C and 6A). O.: tergite VII, between muscles 1 and 2, more posterior; I.: tergite VIII, between the fibres of muscle 1; F.: retractor of segment VIII.

5: *M. antecosta-antecostalis urosterni VII* (Fig. 5A–C). O.: paramedially near the anterior margin of sternite VII; I.: anterior margin of hemi-sternite VIII; F.: retractor of segment VIII.

7: not named (Figs. 5B, C and 6A, B). O.: anterior half of tergite VII with 2 portions which unite a short distance before the insertion site, close to the lateral margin; I.: anterior margin of hemi-sternite VIII, close to the lateral margin; F.: probably mainly as retractor of segment VIII. A muscle in a corresponding position is depicted in von Kéler (1963) (Plate XXVI, Fig. 4c, muscle 183), but the description of 183 in the list of muscles therein does not match with the figure.

8: *M. urotergo-sternalis VII* (Fig. 6A and B). O.: near the lateral margin of tergite VII, with 2 large heads; I.: sternite VII, with 2 separate attachment areas; F.: segment VII – depressor.

10: *M. antecosta-antecostalis uronotum medialis VIII* (Figs. 5A–C and 6A, B). O.: paramedially on the anterior region of tergite VIII; I.: paramedially on the anterior margin of hemi-tergite IX; F.: retractor of segment IX.

11: *M. antecosta-antecostalis uronotum lateralis VIII* (Figs. 5A–C and 6A, B). O.: anterior region of tergite VIII, close to the lateral margin; I.: anterior margin of hemi-tergite IX, close to the lateral margin; F.: retractor of segment IX.

13: *M. antecosta-antecostalis urosterni VIII* (Fig. 5C). O.: paramedially close to the anterior margin of hemi-sternites VIII; I.: anterior margin of hemi-sternites IX; F.: retractor of segment IX.

15: *M. urotergo-sternalis VIII* (Fig. 5C). O.: close to the lateral margin of tergite VIII, with 2 distinct portions; I.: hemi-sternites VIII, with 2 portions; F.: segment VIII – depressor.

21: *M. urotergo-sternalis IX* (Fig. 5B). O.: hemi-tergites IX; I.: hemi-sternites IX; F.: depressor of segment IX.

24: *M. urotergo-phallicus (medialis)* (Fig. 6B). O.: tergalapodeme; I.: laterally on the paramere; F.: unclear.

27: not named (Fig. 5A and B). O.: tergal apodeme IX (pleurite IX?), dorsally on the anterior region; I.: hemi-sternites IX; F.: retractor of hemi-sternites IX.

28: *M. tergapodemo-phallobasicus major* (Figs. 5A, B and 6A, B). O.: tergal apodeme IX (pleurite IX?), dorsally on the anterior region, in front of muscle 17; I.: parameres; F.: abductor of the parameres.

46: *M. phallobaso-phallopodemalis* (Figs. 5A and 6A, B). O.: sclerotised rods at the basal part of the penis; I.: medially on the parameres; F.: protruder of the penis.

51: *M. phallopodemo-endophallicus (dorsalis)* (Fig. 5A). O.: phallobase; I.: roof of the endophallus; F.: endophallus retractor.

61: not named (Fig. 5A and B). This transverse muscle connects the pleurites of segment VII, a short distance anterad the posterior margin of the segment. It is located above tergite VIII.

62: not named (Fig. 5A–C). A transverse muscle bundle connecting the anteroventral corners of tergite VIII. It lies below the hemi-sternites of segment IX.

3.3. Internal parts of the genital system (overview: Fig. 7)

3.3.1. Testes

The paired testes are slender, multi-coiled tube-like structures and reach far into the anterior part of the abdomen (segment V or even IV) (Figs. 3, 7 and 8F). The epithelium is formed of cubic cells.

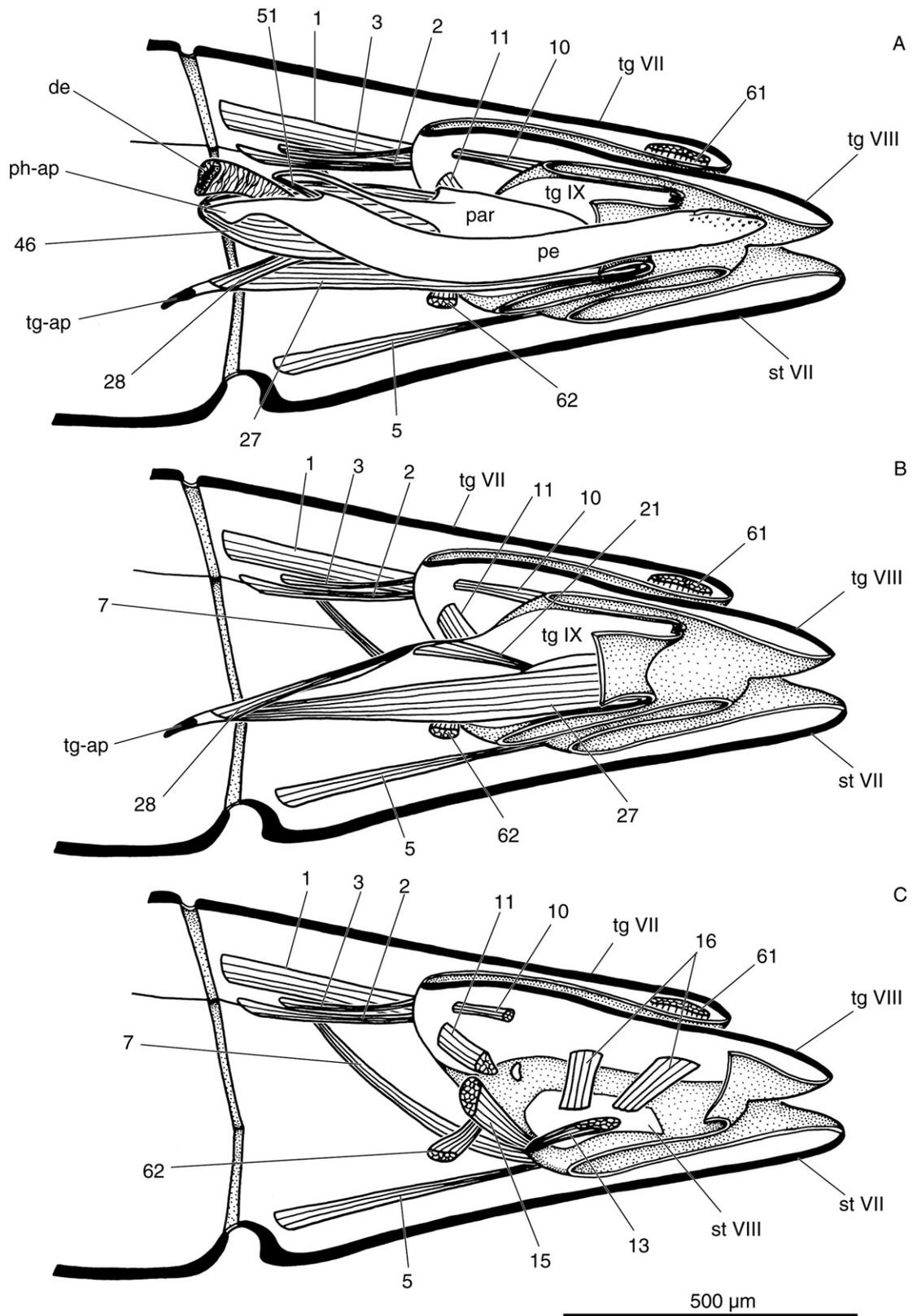


Fig. 5. *T. bruchi*, male postabdomen, skeleto-muscular arrangement. A cut along the medio-sagittal line; B as in A, but aedeagus removed; C as in B, but segment IX removed. de, ejaculatory duct; par, paramere; pe, penis; ph-ap, pallapodeme; st, sternite; tg, tergite; tg-ap, tergal apodeme.

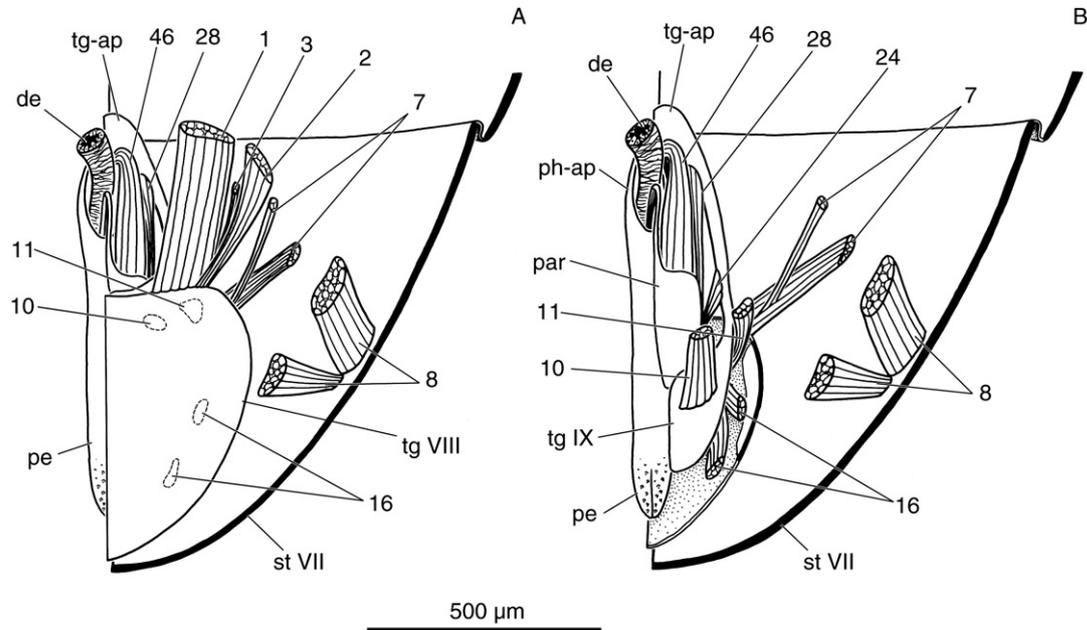


Fig. 6. *T. bruchi*, male postabdomen, skeleto-muscular arrangement. (A) Dorsally opened, tergite VII removed; (B) as in A, but tergite VIII removed. de, Ejaculatory duct; par, paramere; pe, penis; ph-ap, pallapodeme; st, sternite; tg, tergite; tg-ap, tergal apodeme.

The nuclei are very large, almost completely filling out the basal third of the cells. The lumen of the testes is densely filled with spermatozoa. An external muscularis consisting of 6–8 layers of circular fibres is present.

3.3.2. Vas deferens

The paired vasa deferentia are short, stout tubes. The epithelium is formed of small, cubic cells with comparatively large nuclei. The

lumina contain spermatozoa and secretions. The muscularis is composed of 1–2 layers of circular fibres.

3.3.3. Ejaculatory duct

The vasa deferentia are connected with the unpaired, median ejaculatory duct directly (Figs. 7 and 8C, D) in front of the aedeagus. Three successive regions of the ejaculatory duct can be distinguished, differing morphologically and histologically. The most proximal region, outside the aedeagus, is equipped with an epithelium of very large, irregularly shaped cells with the large nuclei in various positions. The lumen is narrowed by extensive folds of the epithelium. The muscularis consists of 1–2 circular and a few longitudinal fibre layers. The second region (mid-region) closely resembles the first in most aspects, but the muscularis is reduced to a single layer of circular fibres. In the third region, inside the closed aedeagal tube, the epithelial cells are much smaller, ca. 1/2 to 1/4 the size of those in the proximal regions. The lumen is wide. The duct is surrounded by a loose meshwork of single muscle fibres.

3.3.4. Accessory glands

The accessory gland openings are located in the boundary region of the testes and the vasa deferentia. The paired glands are bilobed; each lobe has the form of an elongated sac (Fig. 7). The epithelium is formed of cubic cells with the nuclei in most of them close to the basal cell pole. The cytoplasm appears granular. In many cells larger storage compartments are visible. Most of the gland lumen is filled with secretion products which appear light purple in the stained sections.

4. List of phylogenetically relevant characters

Characters with potential value for phylogenetic reconstruction are listed in the following in a morphology based sequence (see Section 3). The informations on the other taxa were mainly taken from the following contributions: Aspöck and Aspöck (2008) (*Sialis*, *Dysmicohermes*), Beutel and Lawrence (2005) (Coleoptera in general), Edwards (1950) (*Amphizoa*), Edwards (1953a,b) (*Priacma*), Hieke (1966) (*Harpalus*, *Geotrupes*, *Liparus*), Hörnschemeyer (2009) (*Crowsoniella*, *Micromalthus*), Lawrence, 1999 (*Omma*), Lawrence et al. (2010)

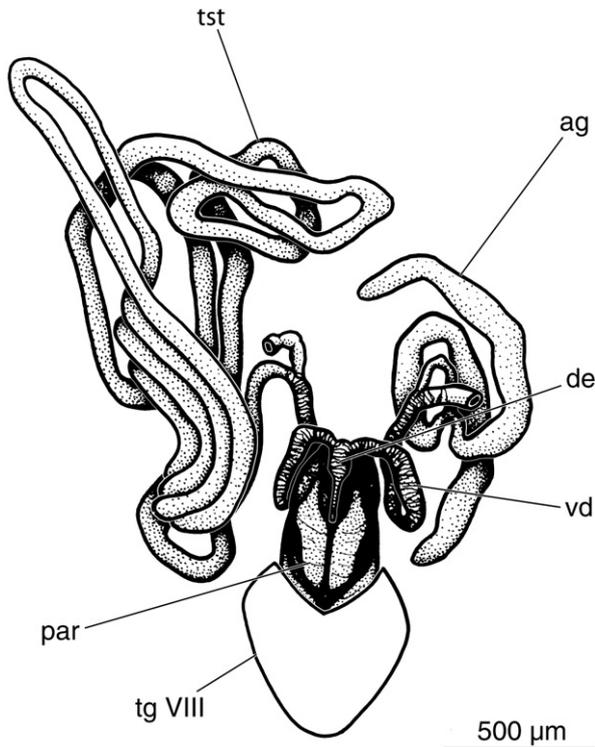


Fig. 7. *T. bruchi*, internal parts of the genital system, dorsal view; left accessory gland and right testis removed. ag, accessory gland; de, ejaculatory duct; par, paramere; tg, tergite; tst, testis; and vd, vas deferens.

Table 1

List of muscles found in *Tetraphalerus bruchi* and comparison with the muscular equipment of other beetles and a megalopteran. Ch, Chauliodes; Te, Tetraphalerus; An, Andogyrus; Ha, Harpalus; Ge, Geotrupes; Li, Liparus. Bold values indicate the state in Tetraphalerus.

No	Hieke (1966) (largely adopted from von Kéler, 1963)	Maki (1936)	Ch	Te	An	Ha	Ge	Li
1	M. antecosta-antecostalis uronotum medialis VII	249	1	1	1	1	1	1
2	M. antecosta-antecostalis uronotum lateralis VII	250	1	1	1	1	1	1
3	M. uronoto-antecostalis	251	1	1	1	1	0	1
4		252	1	0	0	0	0	0
5	M. antecosta-antecostalis urosterni VII	258	1	1	1	1	1	1
6	M. urosterno-antecostalis VII		0	0	1	1	0	1
7		263/264	1	1	0	0	0	0
8	M. urotergo-sternalis VII	265	1	1	1	1	1	1
9	M. sterno-pleuralis VII		0	0	1	1	1	1
10	M. antecosta-antecostalis uronotum medialis VIII	294	1	1	?	1	1	1
11	M. antecosta-antecostalis uronotum lateralis VIII		0	1	1	1	1	1
12	M. uronoto-antecostalis VIII	295	1	0	1	1	1	1
13	M. antecosta-antecostalis urosterni VIII	296	1	1	1	1	1	1
14	M. urosterno-antecostalis VIII		0	0	?	1	0	0
15	M. urosterno-tergapodemalis	297	1	1	1	1	0	1
16	M. urotergo-sternalis VIII	298 + 299	1	1	1	1	1	1
17	M. sterno-pleuralis VIII		0	0	0	0	1	0
18		303	1	0	0	0	0	0
19		304	1	0	0	0	0	0
20		305	1	0	0	0	0	0
21	M. urotergo-sternalis IX	308 (?)	1	1	?	1	1	0
22	M. urotergo-phallobasicus superior		0	0	0	1	0	0
23	M. urotergo-phallobasicus inferior		0	0	0	1	0	0
24	M. urotergo-phallicus medialis		0	1	0	1	0	1
25	M. urotergo-phallicus lateralis		0	0	0	1	0	0
26	M. tergo-paratergalis IX	307	1	0	0	0	(1)	0
27			0	1	0	0	0	0
28	M. tergapodemo-phallobasicus major	306	1	1	1	1	1	1
29	M. tergapodemo-phallobasicus minor		0	0	0	1	0	1
30	M. tergapodemo-phallobasicus medialis		0	0	0	1	0	0
31	M. tergoapodemo-phallobasoapodemalis medialis		0	0	0	0	1	0
32	M. tergoapodemo-phallobasoapodemalis lateralis		0	0	0	0	1	0
33	M. urosterno-tergoapodemalis		0	0	0	0	0	1
34	M. urosterno-phallobasicus		0	0	0	0	0	1
35	M. phallobasoapodemo-phalloapodemalis superior		0	0	0	0	1	0
36	M. phallobasoapodemo-phalloapodemalis inferior		0	0	0	0	1	1
37	M. phallobasoapodemo-phalloapodemalis basalis		0	0	0	0	1	0
38	M. phallobasoapodemo-phallobasicus superior		0	0	0	0	1	0
39	M. phallobasoapodemo-phallobasicus medialis		0	0	0	0	1	0
40	M. phallobasoapodemo-phallobasicus inferior		0	0	0	0	1	0
41	M. phallobasoapodemo-phallicus		0	0	0	0	1	0
42	M. tergoapodemo-phallicus dexter		0	0	0	1	0	0
43	M. tergoapodemo-phallicus sinister		0	0	0	1	0	0
44	M. phallobasicus		0	0	0	1	0	1
45	M. interphalloapodemalis		0	0	0	0	0	1
46	M. phallobaso-phalloapodemalis		0	1	?	1	1	1
47	M. phallobaso-phallicus		0	0	0	0	1	0
48	M. phallobasoapodemalis		0	0	0	0	1	0
49	M. phallobaso-endophallicus		0	0	0	0	0	1
50	M. phalloapodemo-ductalis		0	0	0	0	0	1
51	M. phalloapodemo-endophallicus (dorsalis)		0	1	0	1	0	1
52	M. phalloapodemo-endophallicus longus		0	0	0	0	0	1
53	M. phalloapodemo-endophallicus brevis		0	0	0	0	0	1
54	M. phalloapodemo-endophallicus basalis		0	0	0	0	0	1
55	M. phallo-ductalis		0	0	0	0	1	0
56	M. phallobasicus externus		0	0	0	0	1	0
57	M. phallobasicus internus		0	0	0	0	1	0
58	M. phalloapodemalis internus		0	0	0	1	0	0
59		309	1	0	0	0	0	0
60		310	1	0	0	0	0	0
61			0	1	0	0	0	0
62			0	1	0	0	0	0
Total			20	18	<20	28	29	28
Assymetric terminalia			–	–	–	+	+	+
Torsion in copula			–	–	–	+	+	+

(Coleoptera in general), Maki (1936) (*Chauliodes*), Navarrete-Heredia et al. (2005) (*Lepicerus*), Nyholm (1969) (*Cyphon*), Nyholm (1972) (*Helodes*), Pace (1975) (*Crowsoniella*), Reichardt (1973) (*Ytu*), and Vulcano and Pereira (1975) (*Omma*, *Paracupes*, *Cupes*, *Priacma*) (see Table 2).

Characters 5, 7, and 9–14 are scored as inapplicable (–) for the megalopteran *Chauliodes* at the present stage, as the homology of the sclerites involved in the formation of the coleopteran aedeagus with terminal sclerites found in megalopterans (which lack an aedeagus) remains highly ambiguous.

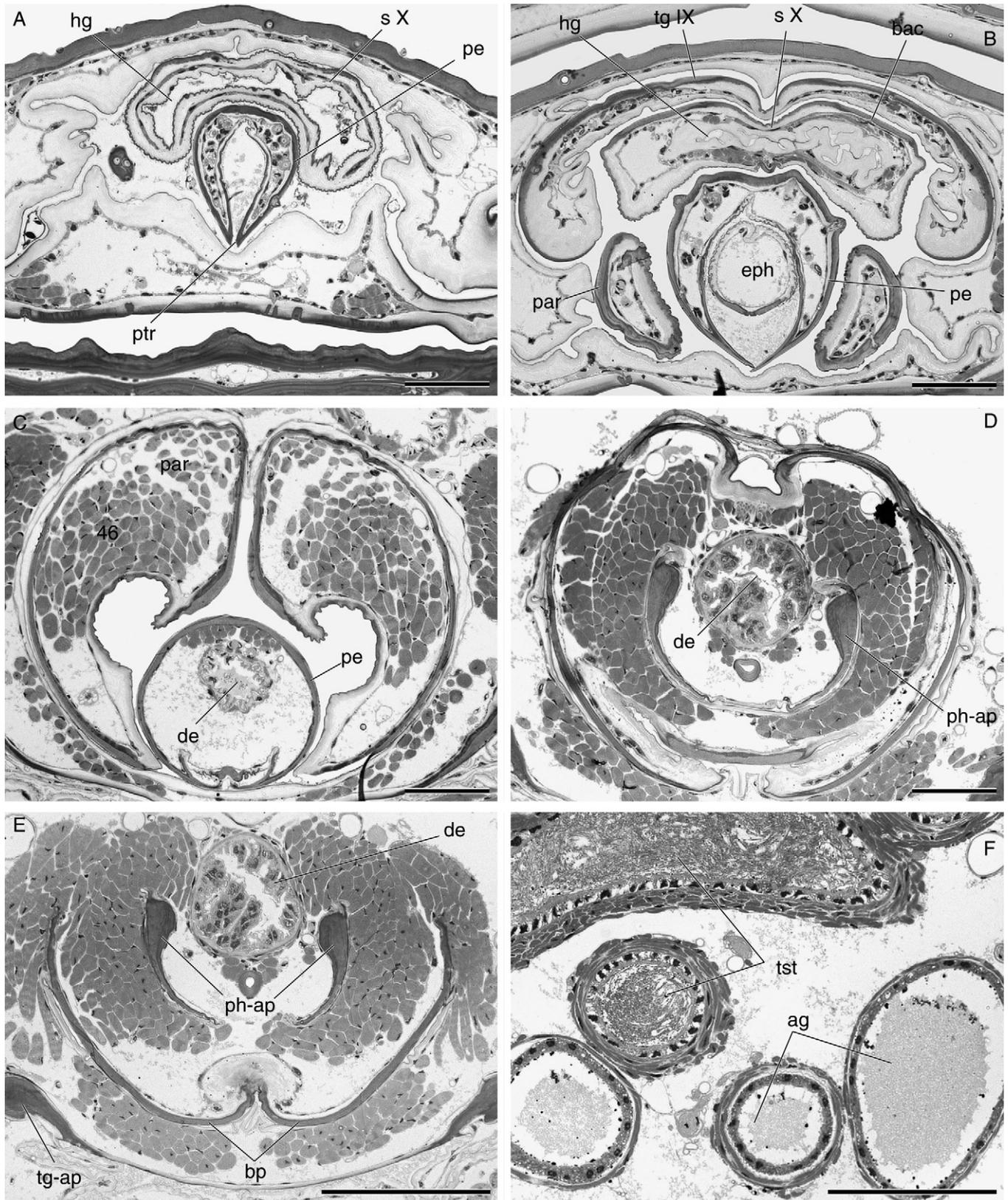


Fig. 8. *T. bruchi*, male postabdomen and internal parts of the genital system, histological cross-sections. (A) Distal part of the penis with phallosome, segment X; (B) mid-part of the penis, parameres, segment X with baculi, tergite IX with dorso-medial cleft; (C) proximal part of the parameres; (D) phallapodemes; (E) sclerotized basal piece; (F) testes. ag, accessory gland; bac, baculi; bp, basal piece; de, ejaculatory duct; eph, endophallus; hg, hindgut; par, paramere; pe, penis; ph-ap, phallapodeme; ptr, phallosome; s, segment; tg, tergite; tg-ap, tergal apodeme; tst, testes. Scale bar: 100 μ m.

Table 2

Character state matrix showing distribution of character states. ‘–’ designates inapplicable characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Sialis</i>	0	0	0	0	–	0	–	2	–	–	–	–	–	–	0
<i>Chauliodes</i>	0	0	0	0	–	0	–	2	–	–	–	–	–	–	0
<i>Dysmicohermes</i>	0	0	0	0	–	0	–	2	–	–	–	–	–	–	0
<i>Tetraphalerus</i>	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1
<i>Omma</i>	1	?	?	1	1	?	0	0	(1)	(1)	0	?	1	0	?
<i>Paracupes</i>	1	(1)	(2)	?	?	?	?	0	?	?	1	?	0	0	?
<i>Cupes</i>	1	0	?	1	?	?	0	0	1	3	0	1	0	0	?
<i>Priacma</i>	1	?	1	1	1	1	2	0	1	3	2	1	0	0	?
<i>Crowsoniella</i>	1	?	1	1	1	1	3	0	(1)	(1)	2	1	0	1	?
<i>Micromalthus</i>	?	?	?	?	?	0	?	0	?	?	?	?	?	0	?
<i>Lepicerus</i>	0	0	?	?	?	?	?	1	0	–	0	0/2	2	3	0
<i>Ytu</i>	?	?	?	?	?	?	?	1	0	–	0/1	0	3	0	0
<i>Andogyrus</i>	0	0	1	1	1	1	0	0	1	2	0	0	0	2	1
<i>Amphizoa</i>	1	2	1	1	1	0	1	0	1	0	1	1	0	0	?
<i>Harpalus</i>	1	3	2	1	1	2	0	0	0	–	0	2	0	0	1
<i>Cyphon</i>	1	?	0	1	0	0	0	1	0	–	0	0	–	–	0
<i>Geotrupes</i>	0	0	0	1	1	0	1	0	1	2	0	2	0	0	0
<i>Liparus</i>	1	1	–	–	–	0	–	0	1	2	0	2	2	0	0

- Exposure of sternite VIII: (0) not retracted in repose, permanently exposed; (1) retracted in repose. Sternite VIII is retracted in repose in most beetles considered here, except for *Lepicerus*, *Andogyrus* and *Geotrupes*. In the megalopteran representatives, sternite VIII is permanently exposed.
- Sclerotization of sternite VIII: (0) ventro-median plate without modifications; (1) pair of small ventro-lateral plates; (2) ventro-median plate with deep posteromedian incision; (3) transverse clasp with a pair of caudo-lateral lobes. The sclerotized part of sternite VIII is restricted to a pair of small ventro-lateral plates in *Tetraphalerus*, *Liparus*, and seemingly also in *Paracupes* (Vulcano and Pereira, 1975, Fig. 27), but critical re-examination is required in this case. A deep postero-median incision is found in *Amphizoa*. In *Harpalus*, the venter-VIII sclerotization has the shape of a transverse clasp with paired caudo-lateral lobes.
- Sclerotization of tergite IX: (0) unpaired dorsal plate; (1) divided along the dorsal midline; (2) division incomplete, with deep median incision. Tergite IX is divided along the dorsal midline in *Tetraphalerus*, *Priacma*, *Crowsoniella*, *Andogyrus* and *Amphizoa*. A deep median incision is reported from *Harpalus* and is depicted for *Paracupes* (Vulcano and Pereira, 1975, Fig. 27). However, the character has to be checked critically for *Paracupes*. The character is scored inapplicable if no tergite IX - sclerotization is developed (*Liparus*).
- Anterior apodemes of tergite IX (tergal apodemes): (0) absent; (1) present. Tergal apodemes are present in almost all coleopteran representatives considered in this study. Scored as inapplicable if no tergite IX – sclerotization is present (*Liparus*). The tergal apodemes are considered as the pleural plates of segment IX by some authors (e.g., Edwards, 1950).
- Ventromedian fusion of tergal apodemes: (0) not fused; (1) ventromedially fused. The tergal apodemes are fused ventromedially in *Tetraphalerus*, *Omma*, *Priacma*, *Crowsoniella*, *Andogyrus*, *Amphizoa*, *Harpalus* and *Geotrupes*. They are clearly separated in *Cyphon*. Scored as inapplicable if tergal apodemes are not developed (Megaloptera), or if no tergite IX – sclerotization is present (*Liparus*).
- Sclerotization of sternite IX: (0) unpaired, ventromedian plate; (1) divided into a pair of hemi-sternites; (2) asymmetrical, small plate. The sternite IX - sclerotization is divided into a pair of 'hemi-sternites' in *Tetraphalerus*, *Priacma*, *Crowsoniella* and *Andogyrus*. It is an asymmetrical and small sclerotised plate in *Harpalus*.
- Fusion of sternite IX with tergal apodemes: (0) clearly separated by membranous areas; (1) fused with tergal apodeme by ventromedian sclerotised band; (2) fused with the tergal apodeme by latero-ventral sclerite bands; (3) extensive fusion in the pleural area. The tergal apodemes are fused with sternite IX by an unpaired ventromedian sclerite band in *Amphizoa* and *Geotrupes*. Both elements are connected by paired ventro-lateral sclerite bands in *Priacma*. An extensive fusion in the pleural area is reported for *Crowsoniella* (Pace, 1975). Scored as inapplicable if no tergal apodemes are developed (Megaloptera), or if a tergite IX – sclerotization is lacking (*Liparus*).
- Aedeagus: (0) trilobed (parameres and penis) (1) reduction of parameres; (2) no aedeagus developed. In most of the beetle taxa considered here a trilobed aedeagus is present. This is not the case in myxophagans and *Cyphon*, which have the parameres reduced to varying degrees. An aedeagus in the strict sense is lacking in the megalopteran taxa.
- Phallobase distinctly sclerotized ('basal piece'): (0) no; (1) yes. The phallobase is distinctly sclerotised in *Tetraphalerus*, *Cupes*, *Priacma*, *Andogyrus*, *Amphizoa*, *Geotrupes* and *Liparus*. A sclerotized basal piece is probably also present in *Omma stanleyi* (Vulcano and Pereira, 1975, Fig. 29) and *Crowsoniella* (Pace, 1975). However, the situation deserves a critical re-examination for these two taxa. Scored inapplicable if an aedeagus in the strict sense is not developed (Megaloptera).
- Shape of basal piece: (0) small ventromedian plate; (1) large, extended to the lateral areas; (2) ring-like; (3) dorsal and ventral clasp-like sclerite band, both fused. The sclerotized basal piece is large and extended to the lateral areas of the phallobase in *Tetraphalerus* and probably also in *Omma* and *Crowsoniella*. It is ring-like, encircling the entire phallobase in *Andogyrus*, *Geotrupes* and *Liparus*. A dorsal and a ventral clasp-like sclerite band, both fused together, are found in *Cupes* and *Priacma*. Scored as inapplicable if an aedeagus is not developed (Megaloptera), or if no distinct sclerotization of the phallobase is present (Myxophaga, *Harpalus*, *Cyphon*).
- Shape of penis: (0) short, stout; (1) long and slender; (2) laterally flattened. The penis is long and slender in *Tetraphalerus*, *Paracupes* and *Amphizoa*. In the genus *Ytu*, two alternative conditions can be observed: either a short and stout, or a long and slender penis. The penis is laterally flattened in *Priacma* and *Crowsoniella*. Scored as inapplicable if a penis is not developed (Megaloptera).
- Curvature of penis: (0) symmetrical, straight; (1) symmetrical, posterior part slightly bent dorsad; (2) asymmetrical. The penis is symmetrical, with the posterior part slightly bent dorsad in *Tetraphalerus*, *Cupes*, *Priacma*, *Crowsoniella* and *Amphizoa*. It is asymmetrical in *Harpalus*, *Geotrupes*, *Liparus* and one of the

- Lepicerus*-species (*L. inaequalis*). Scored as inapplicable if a penis is not developed (Megaloptera).
13. Shape of parameres: (0) without notch; (1) notched, sclerotized proximal and membranous distal part clearly distinguishable; (2) small, plate-like; (3) rudimentary, tube-like. The parameres are deeply notched, displaying a sclerotized proximal and a membranous distal part in Ommatidae. They are small and plate-like in *Lepicerus* and *Liparus*. The parameres are reduced to small, tube-like appendages in *Ytu* (some species totally lack parameres). Scored as inapplicable if parameres are absent (*Cyphon*, Megaloptera).
 14. Fusion of parameres: (0) not fused; (1) basal parts dorsomedially fused; (2) basal parts ventromedially fused; (3) ring-like fusion of basal parts. The basal parts of the parameres are dorso-medially fused in *Crowsoniella*, ventro-medially in *Andogyrus*, and ring-like in *Lepicerus*. Scored as inapplicable if parameres are absent (*Cyphon*, Megaloptera).
 15. Testes: (0) compact, follicular; (1) tubular, coiled. The testes are tubular and multi-coiled in *Tetraphalerus* and in the adephagan representatives examined so far. This character deserves further scrutiny, in particular in Archostemata.

5. Discussion

The pregenital segments are not the main topic of this study and will not be discussed in detail here. An obvious autapomorphy of Coleoptera s.l. is the far-reaching reduction of sternite I and the structural modification of sternite II (e.g., Crowson, 1981; Beutel et al., 2008). This is likely linked with the specific condition of the metacoxae, which are usually transverse and abutting with the ventral abdominal base, in contrast to other holometabolous lineages, where they are more or less prominent (Friedrich and Beutel, 2010). The retracted condition of the terminal segments (tergites IX and X, sternites VIII and IX) is another autapomorphy of Coleoptera (e.g., Crowson, 1981; Beutel and Haas, 2000). This is apparently part of the entire mechanical protection strategy which obviously played a crucial role in the evolution of beetles (e.g., Beutel, 1997). With respect to the abdominal pleurites, *Tetraphalerus* (as other archostematan beetles) belongs to the haplogastran type (see Crowson, 1955), which is apparently the plesiomorphic condition in Coleoptera.

The male postabdomen of *Tetraphalerus* appears less derived than in the vast majority of Coleoptera: the sclerotised elements are arranged symmetrically and show no stronger modifications, as asymmetries or fusions. The aedeagus is trilobed (paired lateral parameres and a median penis), which is generally considered as plesiomorphic (e.g., Lawrence et al., 2010). All elements of the copulatory apparatus, i.e. the phallobase with a sclerotised basal piece, the parameres and the penis, are well developed and easily distinguishable. The muscular equipment is simple and moderately developed compared to what is reported from other beetles (e.g., *Harpalus*, *Geotrupes*, *Liparus*; Hieke, 1966; *Melolontha*, Krell, 1996), with only 18 identified muscles. All muscles (except the transverse muscles 61 and 62) occur pairwise and symmetrically. The homology of at least 12 of the muscles found in the male postabdomen of *Tetraphalerus* with muscles reported from the megalopteran *Chauliodes formosanus* Petersen (Maki, 1936) can be established with reasonable certainty. The enormous increase of the number of postabdominal muscles in representatives of the higher lineages of Coleoptera (*Harpalus*: 28 muscles, *Geotrupes*: 29 muscles, *Liparus*: 28 muscles) is linked with a condition which is found throughout these groups: a torsion of the copulatory apparatus of 90° in repose and of 180° in copulation. As a consequence, the terminal sclerites are arranged in a more or less asymmetric manner, and more muscles are required as the

movements carried out during copulation are more complex. Within Adephaga, *Harpalus* displays both conditions, the asymmetry and torsion, and a high number of 28 postabdominal muscles, many of them not occurring pairwise in both body halves or arranged asymmetrically. A similar condition is found in all groups of Adephaga (e.g., *Dytiscus*; Korschelt, 1923, 1924; see also Beutel and Roughley, 1988) except for Gyrinidae, which arguably represent the sister taxon to all remaining adephagan families (Beutel and Roughley, 1988; Beutel and Lawrence, 2005; Dressler and Beutel, 2010; but see also Shull et al., 2001; Maddison et al., 2009). In strict contrast to the other groups of Adephaga, the male postabdomen of gyridid beetles (*Andogyrus*, F. Hünefeld, pers. obs.) is symmetrical and a torsion does not take place. Only about 20 postabdominal muscles are present, and all of them occur pairwise and are symmetrically arranged. In Myxophaga, symmetrical and asymmetric terminalia occur within one family (Lepiceridae; Navarrete-Heredia et al., 2005). Muscle data are not available yet for this suborder. In most families of Polyphaga, the terminalia are of the symmetric type. Notable exceptions are Staphylinidae (Peschke, 1978), Cucujiformia and Scarabaeoidea (summary in Krell, 1996, p. 21). The arrangements of sclerites as well as the musculature differ in many details between the coleopteran groups with asymmetric terminalia. In *Harpalus*, *Geotrupes* and *Liparus* only few postabdominal muscles can be homologised with reasonable certainty. The asymmetry as well as the torsion of the terminal segments clearly represent derived conditions, which evolved several times independently within the coleopteran suborders. The ancestral condition of Coleoptera and each of the suborders is most likely a symmetric, largely unmodified postabdomen with a comparatively simple set of muscles. The extruded terminal parts are simply bent downwards for penetration of the female. Presently, the knowledge of the male postabdominal musculature is far too fragmentary to be included in a formal cladistic analysis. Investigations on the postabdomen and its musculature of representatives of Helodidae and Scirtidae, as polyphagan beetles with a symmetric postabdomen, would be an obvious next step to contribute to a reliable phylogenetic and evolutionary interpretation (for the sclerotized parts of Helodidae see Nyholm, 1969, 1972; for Scirtidae see Lawrence, 2005).

The published data on internal soft parts of the male genital apparatus are very fragmentary at present (e.g., Breland and Simmons, 1970; Calder, 1990; Noirot and Quennedy, 1991) and some of the studies only provide a more or less general overview as they are based on simple dissection techniques (e.g., Opitz, 2003). The available information is clearly insufficient for a reliable phylogenetic interpretation. One internal element of the reproductive system, the testes, shows an interesting pattern among the beetle suborders. The testes of *Tetraphalerus* are long, multi-coiled tubes (see also Crowson, 1981, Fig. 95) and a similar same condition is reported from *Prolixocupes* (Vidal Sarmiento, 1969), the myxophagan genus *Torrudincola* (Reichardt, 1973) and from adephagan males studied so far (see Crowson, 1981). Only Polyphaga display the follicular type (e.g., Lawrence, 1982). One explanation would be to consider this as the result of a character reversal, and the tubular condition as an autapomorphy of Coleoptera. An alternative scenario would be the maintainment of the ancestral condition in Polyphaga, and the derived character state as a potential synapomorphy of the non-polyphagan suborders (see Kukulova-Peck and Lawrence, 2004).

The number of characters with potential phylogenetic value presented here is comparatively low (15 characters), compared with other character systems (see Beutel and Haas, 2000; Beutel et al., 2008; Friedrich et al., 2009; Hörnschemeyer, 2009). The difficulty in establishing phylogenetically informative characters of

the male postabdomen is partly due to the lack of reliable data for most taxa, in particular on the postabdominal musculature. Another reason is the immensely high degree of variation of the skeletal elements, which makes homology assessments within Coleoptera and across the holometabolous orders very difficult.

The following part of the discussion is based on tree topologies obtained in recent analyses of larger data sets (e.g., Beutel et al., 2008, in press; Friedrich et al., 2009; Hörnschemeyer, 2009 [Archostemata, coleopteran suborders]; Wiegmann et al., 2009 [Holometabola]).

The position of *Tetraphalerus* as sistergroup of *Omma* is well established (e.g., Lawrence, 1999; Beutel et al., 2008). A likely synapomorphy of the male postabdomen is the presence of a deep notch on the parameres, which are divided into an extensively sclerotized proximal portion and a membranous distal part. Differences are obvious regarding the position of the notch: the distal portion is approximately 1/4 as long as the entire paramere in *Tetraphalerus* and *Omma stanleyi*, but only 1/6 as long in *Omma rutherfordi* and *Omma mastersi* (see Lawrence, 1999). The latter condition may possibly represent a synapomorphy of the two species. Moreover, in dorsal view the parameres are more or less straight in *Tetraphalerus* and *O. stanleyi*, but the distal portions are markedly curved towards the median line in *O. rutherfordi* and *O. mastersi*. The penis of *Tetraphalerus* is long and slender, by far exceeding the parameres in length caudally. In contrast to this, the penis is markedly shorter than the parameres in all species of *Omma*, and much stouter in *O. rutherfordi* and *O. mastersi* compared to the intermediate condition in *O. stanleyi* (Lawrence, 1999; Vulcano and Pereira, 1975). Different degrees of shortening of the penis may be considered as an autapomorphy of the genus *Omma*, and a synapomorphy of *O. rutherfordi* and *O. mastersi*, respectively. In its overall design, the exoskeletal parts of the male postabdomen of *Tetraphalerus* comes closest to the condition in *O. stanleyi*, which is likely due to preserved plesiomorphic features.

In two recent morphology-based studies on Archostemata, Ommatidae were placed as the sister group of all other extant families of the suborder (Beutel et al., 2008; Friedrich et al., 2009). The overall simple and unspecialized condition is in agreement with this phylogenetic concept. The terminal segments are not fused and segmental limits are clearly traceable up to segment X. The segments are symmetrical and retracted into each other in repose. The copulatory organ (aedeagus) is composed of the phallobase, the unpaired median penis, and a symmetrically arranged pair of parameres laterad of the penis. All these elements involved in the formation of the aedeagus are comparatively simply shaped and show no distinct modifications, as they are observed in many lineages of Coleoptera (e.g., fusions or reductions of elements, torsions, asymmetries).

A conspicuous feature of *Tetraphalerus* is the well developed sclerotization of the phallobase, the ‘basal piece’. The interpretation of this element is problematic when only traditional morphological techniques are used. After maceration with KOH and hyperextension of the terminalia, the phallobase appears totally translucent, which suggests that it may be extremely weakly sclerotized or membranous. In contrast to this, the ventral and lateral areas of the region of interest appear well sclerotized in SEM-images, with a smooth surface that displays no foldings or irregular surface structures as they are characteristic for SEM images of membranous regions. Images taken with the CLSM show a weak fluorescence of the ventro-lateral parts of the phallobase, an indication that the region is sclerotized, even though less strongly than the parameres or the median lobe. Finally, the examination of the stained histological cross-sections turned out as reliable for an interpretation of the structure in question. The sections clearly show a distinct degree of sclerotization of the basal piece (Fig. 7E). It should be noted in this

context that this sclerotization is also easily visible if the terminalia are extruded without previous maceration (F. Hünefeld, own observations). Maceration, mostly with KOH, and extension of the terminalia is the usual procedure in taxonomic studies, and a possible explanation, why the sclerotized condition of the archostematan phallobase was considered as overlooked a long time (e.g., Lawrence, 1982). A similar condition can be expected in *Omma* (Vulcano and Pereira, 1975, see Fig. 29), and also in *Cupes* and *Priacma*, which possess clasp-like sclerite stripes in the region of the phallobase. However, for further examinations of this character, histological sections are required to allow a reliable interpretation.

Another potential autapomorphy of Archostemata is the median division of the sclerotization of sternum IX, which is conspicuous in *Tetraphalerus*. In Cupedidae, two alternative conditions are found: an unpaired sternal plate is present in most species of this family, but paired ventro-lateral sclerites are found in the small genera *Priacma* (1 sp.) and *Paracupes* (2 spp.). They likely represent the first two branches (or the first branch as a clade) within the family (e.g., Hörnschemeyer, 2009). This suggests that an unpaired sternal plate may have evolved secondarily (autapomorphy of Cupedidae excl. *Priacma* and *Paracupes*), and that the paired sclerites are a groundplan autapomorphy of Archostemata. Alternatively, it cannot be excluded that a subdivision took place two times independently within the suborder.

Several presumably derived conditions found in *Tetraphalerus* have obviously evolved several times independently within Archostemata, and also in other beetle lineages. An apparently apomorphic feature shared by *Tetraphalerus* and *Paracupes* is the reduced condition of the sclerotization of sternum VIII, which is represented by a pair of small ventrolateral plates. Considering the well established monophyly of Ommatidae and Cupedidae (e.g., Lawrence, 1999; Hörnschemeyer, 2009) it is very likely that this feature has evolved independently in the two genera, and also in other groups of Coleoptera. A similar condition is found in Amphizoidae (Edwards, 1950) and the curculionid genus *Liparus* (Hieke, 1966).

The sclerotization of tergite IX is completely divided medially in *Tetraphalerus*, like in the cupetid genera *Paracupes* and *Priacma*, and a deep posteromedian incision is present in *Crowsoniella* (Pace, 1975). Again, well established phylogenetic relationships suggest parallel evolution. However, it cannot be excluded that a secondarily undivided (or partly divided) tergite IX is an apomorphy linking Cupedidae excluding *Paracupes* and *Priacma*. Outside of Archostemata, a divided tergite XI is found in *Amphizoa* (Edwards, 1950) and also in the scirtid *Cyphon* (Nyholm, 1969). A deep posteromedian incision is also present in *Harpalus* (Hieke, 1966).

The anterior margins of the sclerotizations of tergite IX are produced as a pair pair of long apodemes, which are fused ventromedially. This condition is found throughout Archostemata (except *Crowsoniella*) and is widespread within Coleoptera. The presence of these apodemes and probably also the ventro-median fusion represent potential ground plan autapomorphies of the order Coleoptera.

Like in Coleoptera, the male genital apparatus of Holometabola in general, especially the internal soft parts, are very insufficiently known (see e.g., Aspöck and Aspöck, 2008). The information is scattered and very fragmentary (see e.g., Matsuda, 1976). The present study is one step towards a detailed documentation of this character system for a well chosen sample of holometabolan taxa. A documentation and formal phylogenetic evaluation within a broad framework of characters (see Beutel et al., 2010) will likely demonstrate the high phylogenetic value of this system as predicted by Sharp and Muir (1912) and contribute an important mosaic stone to the understanding of the evolution of the “most successful lineage of living organisms” (Kristensen, 1999).

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